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Tundra vegetation change and impacts on permafrost

Monique M. P. D. Heijmans[1†], Rúna Í. Magnússon[1], Mark J. Lara[2,3], Gerald V. Frost[4], Isla Myers-Smith[5], Jacobus van Huissteden[6], M. Torre Jorgenson[7], Alexander N. Fedorov[8], Howard E. Epstein[9], David M. Lawrence[10] and Juul Limpens[1]

[1] Department of Environmental Sciences, Wageningen University & Research, Wageningen, the Netherlands

[2] Department of Plant Biology, University of Illinois, Urbana, IL, USA

[3] Department of Geography, University of Illinois, Urbana, IL, USA

[4] Alaska Biological Research, Inc., Fairbanks, AK, USA

[5] Department of Earth Sciences, Vrije Universiteit Amsterdam, Amsterdam, the Netherlands

[6] School of GeoSciences, University of Edinburgh, Edinburgh, UK

[7] Alaska Biological Research, Inc., Fairbanks, AK, USA

[8] Melnikov Permafrost Institute, Siberian Branch of the Russian Academy of Sciences, Yakutsk, Russia

[9] Department of Environmental Sciences, University of Virginia, Charlottesville, VA, USA

[10] National Center for Atmospheric Research, Boulder, CO, USA

[†]email: monique.heijmans@wur.nl

Abstract

Tundra vegetation productivity and composition are responding rapidly to climatic changes in the Arctic. These changes can, in turn, mitigate or amplify permafrost thaw. In this Review, we synthesize remotely-sensed and field-observed vegetation change across the tundra biome, and outline how these shifts could influence permafrost thaw. Permafrost ice content appears to be an important control on local vegetation changes; woody vegetation generally increases in ice-poor uplands, whereas replacement of woody vegetation by (aquatic) graminoids following abrupt permafrost thaw is more frequent in ice-rich Arctic lowlands. These locally observed vegetation changes contribute to regional satellite-observed greening trends, although the interpretation of greening and browning is complicated. Increases in vegetation cover and height generally mitigate permafrost thaw in summer, yet increase annual soil temperatures through snow-related winter soil warming effects. Strong vegetation–soil feedbacks currently alleviate the consequences of thaw-related disturbances. However, if the increasing scale and frequency of disturbances in a warming Arctic exceeds the capacity for vegetation and permafrost recovery, changes to Arctic ecosystems could be irreversible. To better disentangle vegetation-soil-permafrost interactions, ecological field studies remain crucial, but require better integration with geophysical assessments.

[H1] Introduction

Arctic tundra is changing rapidly, with a pervasive trend toward more abundant and taller vegetation as shrubs and trees expand northward[1]. Field and satellite observations suggest that tundra vegetation has become more productive, a phenomenon known as tundra greening. Such increases in the biomass and stature of Arctic tundra vegetation can alter the thermal properties of the ground surface. Canopies can mediate the effect of increasing summer air temperatures on soil temperatures[2-4] and contribute to insulation of soils in winter through trapping of snow[5-8]. Vegetation and soil characteristics also influence surface energy partitioning and the thermal diffusivity of the soil[9,10].

Permafrost (permanently frozen ground) underlies soil and vegetation, and is the foundation of Arctic tundra ecosystems. In turn, vegetation and near-surface soils insulate permafrost[11], regulating the effects of atmospheric conditions. However, the Arctic is warming more than twice as fast as the global average, amplified by loss of sea ice cover[1]. Even if Arctic temperatures were to stabilize at 2°C of warming, as aimed for with the Paris Agreement, approximately 40% of near-surface permafrost is still projected to thaw[12]. Permafrost-dominated ecosystems are thus at risk[13], even under modest CO_2 emission scenarios[1], with consequences for Arctic inhabitants[14].

Observed tundra vegetation changes are partially related to permafrost thaw, which can be a gradual or rapid process, with differing influences on Arctic ecosystems[15,16] (**Fig. 1**). Gradual thaw could stimulate decomposition of organic soils, releasing soil nutrients[17,18] and encouraging belowground plant responses, changing vegetation productivity and composition[18-20]. Thawing can be abrupt at locations where the ice volume exceeds that of soil pore spaces (excess ice) and forms structures such as ice wedges or ice lenses[16]. When excess ice melts, the soil surface subsides and could even collapse, leading to local mortality and shifts in plant communities[10,16,21,22] as most shrub species cannot tolerate inundated conditions in newly formed depressions[21].

Changes in Arctic ecosystems have the potential to affect global climate[1,23]. Specifically, warming and partial thawing of permafrost soils enhance microbial decay of old soil organic matter[23], estimated to release ∼130–160 Pg carbon, primarily in the form of CO_2, over this century, albeit with large uncertainties[23]. This greenhouse gas release from thawing Arctic soils presents an important climate feedback mechanism for future warming[24-26,27,28], accompanying those associated with albedo changes driven by large-scale increases in tundra shrub cover[9].

In this Review, we describe pan-Arctic patterns of tundra vegetation changes across diverse permafrost environments and their potential effects on permafrost integrity. We begin by documenting Arctic tundra vegetation changes from remote sensing and field observations. We follow with discussion of vegetation-permafrost interactions, including the mechanisms through which vegetation can mitigate or amplify permafrost thaw. Finally, future research priorities are proposed to aid in disentangling the interrelated dynamics of vegetation and permafrost across Arctic environments.

[H1] Arctic tundra vegetation

Climate and other environmental controls, such as topography, soil chemistry, soil moisture and the historical extent of plant species, all influence the distribution and composition of tundra plant communities. Throughout the Arctic tundra biome, there is considerable variation in vegetation productivity and plant species composition from north to south (**Table 1**).

At regional scales, climate is the main factor driving tundra vegetation composition[29]. The tundra biome is treeless by definition, as tree recruitment and growth are limited by stressful conditions because of low summer temperatures (mean July temperature generally < 10°C), low annual precipitation (< 250 mm) and short growing seasons (1.5 - 4 months)[30,31]. Tundra often consists of patchy, low-ground vegetation comprising shrubs, graminoids **[G]** (sedges, grasses, and rushes), forbs, mosses and lichens[31].

Local-scale Arctic tundra vegetation patterns are mostly driven by soil moisture gradients related to landscape microtopography[29]. Poorly drained, high soil moisture locations generally host graminoid vegetation, whereas better drained, more elevated or sloping areas are drier and can be shrub-dominated[31]. Shrubs preferably grow on moist soils[32], but cannot tolerate waterlogged conditions, whereas sedges have adaptations to tolerate anaerobic water-saturated environments.

[H2] Bioclimate subzones

While the northernmost tundra zone is sometimes classified as polar desert[33], tundra vegetation can be green and abundant along the southern margin of the Arctic; the abundance and stature of tundra vegetation generally increases with warmer summer temperatures[30,31,34-36]. This latitudinal variation is often described as bioclimate subzones[31,34-36], as delineated on the Circumpolar Arctic Vegetation Map (CAVM)[31]. The five CAVM bioclimate subzones, A-E from north to south, coincide with increases in summer temperature[31] (**Table 1**) and can be seen as generalized vegetation and climate zonations. In reality, boundaries are diffuse and local deviations are common owing to the influence of local conditions and landscape history[31,36,37].

As demonstrated in the CAVM, the extreme environments of the northernmost part of the Arctic support only scattered cushion plants, forbs, grasses, and a large fraction of mosses and lichens[30,31,37]. Southern Arctic regions, by contrast, host more robust vegetation communities. These include taller deciduous shrub species (willow and alder), and extensive tussock sedge tundra in relatively well-drained (but mesic) parts of the Arctic, such as northern Alaska and north-western Canada[30,31,37]. Given the sensitivity of tundra plant growth to summer temperatures, tundra vegetation generally has, and is expected to continue to increase in abundance and size in a warming climate[38].

[H2] Role of abiotic microgradients

The Arctic tundra biome (as delineated on the CAVM[31]) is underlain by permafrost, generally with a continuous spatial distribution (Supplementary Table 1). The active layer **[G]** is essential to tundra plant life as it forms the rooting zone from which plants can absorb soil-borne nutrients and water in summer[17,39]. Tundra plants often form associations with mycorrhizal fungi that assist with extracting soil nutrients in exchange for carbon[39,40]. Moreover, tundra soils contain diverse microbial communities and over 2,000 species of soil invertebrates[41]. Changes in the soil microbial community can strongly affect the release of carbon and nutrients through decomposition of soil organic matter[41,42]. Differential subsidence and heave in permafrost soils with variable ice content cause additional macro- to micro-scale heterogeneity in topography, soil moisture and thickness of the active layer[16,43,44]. The latter exerts a strong influence on tundra vegetation microgradients[29,43]. Tundra vegetation itself affects permafrost thaw through its influences on the surface thermal regime[2,3,10,45], illustrating the tight linkage between spatial patterns in tundra vegetation and permafrost[4,16,46,47].

[H1] Arctic tundra vegetation change

Both remote sensing and field observations agree over large-scale greening trends in the tundra[38,48-50] (**Fig. 2**). However, relationships between the two still remain poorly understood[50], necessitating documentation of vegetation changes over multiple decades and across diverse Arctic regions.

[H2] Remote sensing observations

[H3] Spectral greening

Expectations that tundra plant communities will develop more green biomass[38] and species distributions will shift northward with warming[48] are corroborated by circumpolar satellite observations. They reveal increasing trends (greening) in the Normalized Difference Vegetation Index **[G]** (NDVI) since the early 1980s[49], with an estimated 20 - 40% of the Arctic tundra showing significant spectral greening[49-51]. This trend likely reflects large-scale increases in vegetation productivity owing to gradual improvement of plant growing conditions related to climate warming[38,50,52,53]. Indeed, experimental warming in 61 tundra sites generally increased vegetation green biomass, with shrub increases in sites with relatively warm air temperatures and graminoid increase in the coldest sites[38].

Warming can increase soil nutrient availability through increased microbial decomposition of soil organic matter, resulting in increased release of plant-available nutrients[54]. Nutrient release is seen as a key mechanism driving the increases in biomass, as evidenced by long-term fertilization experiments[55-57]. Warmer summer temperatures[38,58], longer growing seasons[59], increased precipitation[60], deeper and earlier seasonal permafrost thaw[20,61-63] and increasing atmospheric CO_2

concentrations[64] could all be responsible for increased vegetation productivity. However, the exact mechanisms leading to enhanced tundra vegetation productivity and greening remain uncertain and are likely spatially heterogeneous.

[H3] Spectral browning

Since 2011, spectral greening trends have slowed considerably. In turn, browning **[G]** has become more pronounced locally, with an estimated 1-8% of the Arctic tundra undergoing spectral browning[49-51]. The mechanisms at play are not yet sufficiently clear[49,65], but are often related to specific disturbances that reduce or completely remove vegetation cover[66], including: wildfires, which can dramatically affect vegetation[27,70], surface topography, geomorphology and surface wetness[67-69]; winter warming events, which result in bud break and subsequent freeze damage or frost drought, particularly in low Arctic areas with shallow snow depth[66,70-73]; or herbivores and pathogens[74]. Browning can also be caused by a combination of factors, as demonstrated on the Arctic coast of Alaska where severe spectral browning has been attributed to complex interactions between permafrost landforms, vegetation cover, increasing temperature and precipitation[75].

Browning events related to local disturbances are often followed by vigorous regrowth as plants take advantage of newly available nutrients[46,76]. Gradual greening therefore follows short-lived, often highly local, browning events[50]. In specific cases, however, local browning events can influence the trends in satellite-observed vegetation indices detected at larger spatiotemporal scales[50,77,78]. In Northern Scandinavia, for instance, widespread small-scale browning occurred following climate-related vegetation damage[72]. Similarly, larger scale disturbances such as thermokarst lake expansion, erosion of permafrost coasts and increased flooding are visible in moderate to coarse resolution NDVI[78-80]. As the interaction between disturbance events, recovery and longer-term trends introduces non-linearity in NDVI records, baseline establishment and temporal range and resolution are extremely important in the interpretation of spectral browning.

[H3] Scaling and confounding effects in spectral trends

The relative scarcity of Arctic browning observations could also be related to the spatial resolution of satellite observations; small-scaled browning events are easily overlooked by moderate-resolution satellites owing to spectral mixing[32,50,79,81]. For example, change detection using very high resolution (0.5m) images can reveal small-scale disturbances on sub-decadal timescales that go unnoticed in coarser resolution[84], such as ponding in shrub-dominated tundra[79]. Centimeter-scale NDVI from unmanned aerial vehicles has further been shown to accurately reflect the spatial variation of heterogeneous Arctic ecosystems[77,82]. In Qikqitaruk – Herschel Island, Canada, a 50 x 50 cm pixel size is optimal for detecting variation in NDVI across the landscape[77]. As spatial resolution of space borne sensors has increased, variation in the percentages of spectral greening and browning can often be attributed to the period examined; the longer back in time, the more greening[50,65,83]. As a result, challenges remain in extrapolating the higher-resolution satellite data to larger scale and Arctic-wide greening and browning trends[51,65].

Obtaining suitable satellite data for monitoring high latitude environments is also challenging owing to persistent cloudiness, low solar angles and the short growing season, all of which can result in poor image acquisition[83]. Among satellite-derived vegetation indices, NDVI is the most straightforward to compute and has been most widely used to monitor Arctic ecosystems[49,50,78,80,84]. Although NDVI corresponds well with biophysical vegetation properties in general, increases in surface wetness can reduce NDVI[50,78]. For example, a pixel with increased surface water due to abrupt thaw could show a spectral browning trend, despite vigorous sedge growth in the developing aquatic environment[78].

At the other extreme, NDVI values are relatively insensitive to vegetation changes in very densely vegetated areas, resulting in a non-linear relationship between NDVI values and vegetation green biomass[50]. The largest relative increase in vegetation indices will be found in well-drained locations that have transitioned from bare ground to being vegetated[50]. The greatest NDVI values are typically measured in shrub-dominated plant communities[34,85,86], and in turn, spectral greening has often been linked to expansion of shrub vegetation[50]. However, multi-temporal high-resolution datasets and, ideally, field observations are generally needed to interpret and validate the spectral greening and browning trends for a given location.

[H2] Field observations

[H3] Trends in Arctic vegetation change

Documentation of multi-decadal vegetation changes across diverse Arctic regions remains essential to identify mechanisms of future Arctic vegetation change. Revisiting areas in northern Alaska where old aerial photographs were taken provide some of the earliest reports of increased shrub cover[87,88]. Long-term field monitoring report increasing abundance of graminoid and shrub vegetation[38,48,61,89-91], although it is possible that research finding no change is underreported. Data on vegetation changes are strongly clustered in the Alaskan Arctic, with fewer points available from Eastern Canada, Greenland and the Russian Arctic[38,48,92-96] (**Fig. 2a**). Since this underrepresentation has a role in most synthesis efforts to date[38,48], it is difficult to extrapolate observed trends to a pan-Arctic context. For instance, the Canadian Archipelago and Western Siberia have shown strong browning in satellite observations[49], but very little ground data is available to confirm these trends.

A large part of the observed vegetation change—including shrub cover increase—takes place in dynamic landscape positions (such as floodplains, erosional slopes, permafrost disturbances and drained lake basins) and other landscape locations where exposed mineral soil allows for recruitment of plant species[32,97-99]. Tundra wildfires represent another type of disturbance that tends to support shrub recruitment after initial disturbance[100,101]. Historically, tundra wildfires have occurred with return intervals varying regionally from decades to millennia, but annual burned area could double in the future, based on climate projections[101]. Considering the key role of landscape dynamics and the current gaps in geographical data coverage, future monitoring efforts could improve understanding of vegetation trends across the Arctic and help to relate them to observed spectral greening and browning.

[H3] Analysis of vegetation change across the Arctic

To support insight into regional differences in Arctic tundra vegetation changes, field-observed vegetation cover changes across the Arctic were synthesized (**Supplementary Data**) and related to site characteristics such as bioclimate subzone[31] (**Table 1**), permafrost characteristics, climatic conditions and satellite-based greening trends (**Supplementary Methods**). Based on the reported changes in cover of distinct plant functional groups, sites were subdivided into several commonly observed vegetation change trajectories (**Supplementary Table 2**). For each site, climate re-analysis datasets (1950-2020)[102], NDVI (2000-2020)[103,104] and soil moisture (1987-2020)[105] observations were extracted, based on summer and winter means, and Theil-Sen slopes were calculated to illustrate the changes in site conditions over the recorded period per site. Lastly, thematic data from the CAVM[31] (bioclimate subzone and landscape physiography) and IPA permafrost map[106] (permafrost extent and ice content) were extracted for each site . Relationships between vegetation change trajectories and climate, NDVI and soil moisture data were assessed using ordination techniques, and association between vegetation change trajectories and landscape, permafrost and bioclimate classes per site were assessed using contingency tables and Fisher's exact test.

An increase in shrub cover was by far the most reported vegetation change (46% of sites documenting tundra vegetation change; **Figs. 2a, 2b**) and is relatively uniform over the Arctic tundra (**Figs. 2a, 3a**), although more common in upland than in lowland sites (**Fig. 3b**). Climate, NDVI and soil moisture data and temporal trends are not significantly associated with vegetation change trajectories (**Supplementary Fig. 2**). Instead, different vegetation change trajectories predominate in different bioclimatic subzones (**Fig. 3a**), although scarcity in field data and varying representation per subzone make interpretation of these relationships difficult. Similar to previous synthesis efforts[38,48], the colder Arctic bioclimate subzones A and B are underrepresented (**Fig. 3a**), making it difficult to discern meaningful trends. In bioclimate subzone C (10% of all sites), graminoids and dwarf shrubs **[G]** can establish on newly available soils after glacial retreat[107], though at the cost of the lichen layer at the ground surface[108]. In this cold subzone, increased cover of graminoids and low shrubs are the dominant vegetation changes (**Fig. 3a, Supplementary Table 3 & 4**).

For the southernmost subzones D and E (where most of data points are concentrated), there are many reports of increased cover of tundra shrubs, sometimes replacing graminoids. The reverse also occurs, where low shrub vegetation is replaced by (aquatic) graminoids following abrupt permafrost thaw. Such abrupt thaw-driven vegetation succession (18% of all sites) is relatively common in subzone D (**Fig. 3a**), particularly at sites with ice-rich continuous permafrost (**Fig. 3c**), and was typically observed in coastal lowlands (**Fig. 3b**). Further south in subzone E, tundra vegetation includes tall shrubs **[G]** and reported vegetation changes also include tree establishment. Such tree encroachment (9% of all sites) was most frequently observed in rapidly warming Low Arctic regions in landscape positions with low ice content (**Fig. 3c**). The latter suggests that permafrost characteristics like ice content are an important control on tundra vegetation change trajectories (**Fig. 1**). The absence of significant relationships with the explored climate parameters (**Supplementary Fig. 1**) suggests either strong local control or non-linearity in the response of vegetation composition to changes in environment and climate, supporting the view that Arctic vegetation dynamics are strongly controlled by regional to microscale gradients in permafrost dynamics, topography and wetness.

[H2] Combining datasets

Field-observed vegetation changes are generally assumed to influence the spectral greening trend. However, the vegetation change trajectories described—increased cover of graminoids, increased cover of shrubs, abrupt thaw-driven vegetation succession, and tree encroachment—appear to be associated with similar degrees of spectral greening, as represented by the NDVI (**Fig. 2c**). Moreover, sites with tree encroachment did not show particularly strong spectral greening (**Fig. 2c**). A potential explanation could be that these sites already have abundant shrub vegetation prior to tree establishment, contributing to the non-linearity of NDVI increases in already densely vegetated areas[50].

Abrupt thaw resulted in NDVI trends of similar direction and magnitude as increased shrub cover (**Fig. 2c**). This change could be a result of fast re-colonisation of new vegetation within a decade[46,47,76] or concurrent NDVI increases in adjacent, unaffected vegetation[50]. The positive NDVI trends indicate that the spatial scale of browning events such as abrupt thaw could be too small and short-lived to be detected with trends derived from moderate-resolution satellite imagery[50,65,77]. In addition, NDVI increases could be driven by warming-induced increases in green vegetation cover regardless of the species groups involved[65].

Differences in methods and scale used to assess vegetation cover add to discrepancies between field-based changes in cover of plant functional types and spectral greening. While including cover of dark branches makes mechanistic sense to assess local changes in cover or expansion of species (as done in some field studies), it does not translate directly into changes in green leaf area or leaf area index, which are more closely correlated with spectral greening[49,50]. Regardless, the combination of field observations with large-scale spectral greening leaves no doubt that the Arctic tundra vegetation is changing in many places. With continuing technological developments, the Arctic region can be studied remotely in increasing spatial and temporal detail[77,82,83]. The latter will increase the need for field-based assessments, which are essential for correct interpretation and understanding of the satellite-observed vegetation changes and their impacts on permafrost soils.

[H1] Vegetation–permafrost interactions

Arctic vegetation changes and their impacts on snow conditions have consequences for permafrost integrity[4,10,11]. In general, permafrost occurs in regions with mean annual air temperatures below about -6°C[4]. However, permafrost can locally persist at warmer ambient temperatures and degrade at lower temperatures owing to differences in thermal impacts of vegetation, snow and ground surface of different tundra ecosystems[4,11]. These differences in thermal behaviour depend on interconnected ecosystem properties, such as vegetation, soil, hydrology and microtopography[4,43,47]. Under continued warming, local ecosystem effects on permafrost integrity could become increasingly relevant, as changes in ecosystem properties could mitigate or amplify the influence of air temperature changes on permafrost integrity[4,10].

The exact mechanisms that determine observed thermal effects are not always well understood[10]. Increasing vegetation cover and height result in warmer soil temperatures in winter, but colder soil temperatures and shallower thaw depths in summer (**Table 2**). This effect is evident for shrub vegetation in particular[5]. Manipulation experiments with removal or addition of shrubs, moss and litter confirm the winter warming and summer cooling effects of vegetation[2,6,21,109-112]. The identified mechanisms through which vegetation affects permafrost integrity also vary seasonally **(Fig. 4)**. Effects in winter and spring are strongly determined by vegetation-snow interactions[5,7,8,45,100,113-118], and summer effects revolve around changes in vegetation and ground surface albedo[7,113,119], heat flux partitioning[2,3,6,109,120] and thermal properties of the moss layer and topsoil[4,21,85,111,112,121]. While other mechanisms also likely have a role (**Fig. 4**)[10], snow trapping[7,122] and radiation interception in the canopy[2,6,10] are reported as the main pathways by which tundra vegetation canopies affect permafrost integrity.

[H2] Winter effects

[H3] Snow trapping and insulation by the snowpack

In winter, vegetation primarily affects soil temperatures through trapping of snow in vegetation with taller and more complex canopies, such as tall shrubs[5-7]. As snow is an effective insulator, snow accumulation in shrub canopies will reduce the cooling effect of cold winter air temperatures and lead to warmer winter soil temperatures[5-7,123]. The snow cover in shrub vegetation is not only deeper than outside the shrub canopy, but also differs in physical properties[113,124] that make the snow less conductive to heat[7]. In turn, the warmer winter soil temperature under tall shrub canopies has been hypothesised to provide greater release of soil nutrients in winter through enhanced microbial decomposition of soil organic matter, delivering the nutrients needed for further shrub growth[7,122]. While there is abundant field evidence of taller vegetation trapping more and better insulating snow, resulting in warmer winter soil temperatures[5] (**Table 2**), the strength of the winter effect varies between vegetation types. Winter warming is especially observed under taller shrubs[5], but much less under dwarf shrubs and moss[2,100,110,111] and in cases where microtopography overrides the effect of vegetation on snow depth[21,47,120]. Thus, the extent to which local vegetation structure and microtopography promote snow accumulation likely critically determines the strength of the winter warming effect[7,21,100,125].

[H3] Snow albedo effects

The winter warming effect can be further modified by the snow albedo effect. Apart from its insulative properties, snow has a high albedo and strongly reduces the amount of incoming solar radiation that can melt snow during the Arctic day. The influence of the snow surface albedo is highest for an unbroken cover of snow and varies across the year with greater effects in spring relative to autumn[10,114,124]. However, if shrubs protrude above the snowpack, the albedo can be reduced by around 30% relative to low-lying tundra due to the dark woody stems[8]. The latter can induce temporary snow melt, creating layers of ice within the snowpack[124,126]. Such ice layers increase the density and thermal conductivity of the snowpack and could limit further snow drift in winter[126]. Thus, warm spells in autumn can potentially reduce or cancel out the warming effects of a tall shrub canopy in winter[126].

In spring, the role of albedo becomes pronounced as solar radiation increases after the polar night. The snow albedo effect slows down the melting of snow and warming of the soil in spring[8,45,123,127]. However, when tall shrub branches protrude above the snow, the lower albedo can accelerate the spring snowmelt[122,127,128], cancelling out the soil cooling effect of snow in spring, thereby reinforcing net winter warming.

The winter warming effect of different vegetation types likely depends critically on canopy structure, which determines to what extent vegetation traps snow and protrudes above the snowpack, and thereby the net effect of insulating snow cover and snow albedo effects[114,125,129]. Although there is general consensus that increased tall shrub cover will lead to winter soil warming[5], if and how summer canopy effects on soil temperatures offset these winter warming effects, and under which conditions, remains less well quantified.

[H2] Summer effects

In contrast to winter warming, summer soil temperature recordings and measured thaw depths generally indicate a summer soil cooling effect of taller vegetation (**Table 2**). Daily soil temperatures under different stages of shrub vegetation across the Arctic indicate that summer soil cooling is related to increasing shrub height[5,115] and, for paludifying **[G]** shrublands, to progressive accumulation of insulative organic soil layers[115]. Similar cooling effects are observed for other vegetation types (**Table 2**). In some environments, summer soil temperature in tussock tundra vegetation showed the largest decoupling from summer air temperatures[5], and in one instance, thaw depth was shallower under graminoid vegetation than other tundra vegetation types[116]. Different vegetation types could affect summer soil temperature and permafrost integrity in different ways depending on the mechanism through which they affect the surface energy balance and soil thermal properties[10].

[H3] Summer albedo

The summer surface albedo poses a first control on the surface energy balance. Reflective surfaces such as lichens and standing dead graminoid leaves can increase the albedo[119,130], whereas albedo tends to decline with increasing height and cover of darker vegetation elements, such as shrubs and trees[3,7,119]. Local hydrology can also affect the surface albedo, as ponded areas have low albedos[130]. Therefore, the relative importance of albedo in determining vegetation effects on the soil thermal regime can vary strongly among different settings[130,131].

[H3] Partitioning of solar radiation

Net incoming radiation provides the energy used for warming the air (sensible heat flux), energy used for evapotranspiration (latent heat flux) and energy used for warming the soil (ground heat flux)[132]. Of these fluxes, the ground heat flux ultimately controls soil temperatures and permafrost integrity[3,119,124]. Ground heat fluxes typically account for 5% (forest) to 25% (wet tundra) of total net radiation in northern biomes[3,119]. Over a gradient from barren tundra to forest the proportion of net radiation allocated to sensible and latent heat fluxes tends to increase[3,119,133]. The proportion of net radiation that is allocated to the ground heat flux depends on the degree to which vegetation intercepts incoming radiation and thereby shades the soil surface. The more net shortwave radiation is intercepted higher up in the canopy and available for sensible and latent heat fluxes, the less reaches the ground to contribute to the ground heat flux[119,132,133].

Part of this intercepted net radiation is used for evapotranspiration, which includes transpiration and evaporation from the soil and leaf surface[3]. The latter constitutes a loss of energy in the form of latent heat and leaves less energy available for warming of the surrounding air and soil[3]. Several mechanisms moderate this evaporative cooling effect, such as control of stomatal conductance by plants[124,132,133] and lower soil moisture availability[44,134]. Apart from incoming radiation, Arctic shrub canopies can intercept as much as 15%–30% of ambient rainfall, further contributing to latent heat loss[135,136]. As height and density of vegetation increases, the reference level of energy exchange shifts to a higher position in the canopy, which in practice means that more energy is allocated to sensible and latent heat loss, and less to the ground heat flux[3].

[H3] Canopy aerodynamics

Both sensible and latent heat loss are additionally promoted by the mixing of air, which increases heat transfer between air layers. Compared to smooth short vegetation, taller and more heterogeneous canopies increase air turbulence, and canopy temperatures will be more closely coupled to that of the atmosphere[119,131-133]. However, smooth, low profile shrub canopies have also been found to sustain cool microclimates below the canopy[120,137,138] owing to their dense horizontally branched canopies[120], which can effectively intercept incoming radiation and cool the top soil layer. The cooler surface temperature in turn is decoupled from ambient air temperature due to low air mixing within the smooth, aerodynamic canopy[120,137,138]. The contrast outlined above illustrates the complex role of the canopy structure and its aerodynamic roughness length in flux partitioning. While the turbulence induced by tall rough canopies promotes heat losses to the atmosphere, a lack of turbulence within low densely branched aerodynamic canopies of uniform height creates a smooth vegetation layer acting as an insulator to the underlying soil.

[H2] Soil thermal properties in summer

The ground heat flux is not only determined by the remainder of net radiation after accounting for latent and sensible heat loss but is also modified by the thermal regime of the soil surface[10]. For example, in dry, sparsely vegetated high Arctic environments, ground heat flux can be a relatively large proportion of total net radiation due to low latent heat loss[3,119]. Ground heat fluxes are driven by temperature gradients and influenced by soil thermal diffusivity, the capacity to spread heat into the soil. For example, in wet tundra sites, ground heat fluxes can be substantial, due to the high thermal conductivity of wet soils[3,119]. Soil moisture and organic soil layers provide important controls on the ground thermal regime[4,10].

How vegetation changes affect soil moisture in summer is difficult to quantify. The presence of vegetation can alter the overall soil thermal-hydrological regime by reducing soil moisture due to increased transpiration[120,124,128] and canopy interception[135,136]. These drying effects reduce soil thermal conductivity and thereby the ground heat flux[4,10,136,139,140] . Reduced rain throughfall due to canopy interception can additionally reduce heat inputs into the soil associated with the heat content within the rain itself[140,141]. However, soil moisture and thermal diffusivity are strongly controlled by climate, microtopography and lateral flow, moisture retention characteristics of the soil and organic layers and permafrost extent and ground ice content[10,22,43,47]. Such factors can interact with or even override those of vegetation and cause microscale heterogeneity in wetness, thermal diffusivity and thaw depth[10,29].

Ground surface layers such as plant litter and moss and lichen understories also exert significant controlling influence on thaw depths[109,119,142], as has been illustrated in moss and litter manipulation experiments[109-112]. Mosses often form the understory of tundra vegetation, particularly in wetter tundra regions, and can form thick mats with low thermal conductivity, thus effectively insulating the permafrost[110-112,143]. The insulation depends on the thickness of the moss mat and its moisture status, where moss thermal conductivity has a positive linear relationship with moss moisture content[111], similar to soil organic layers[4,115,144]. In contrast to mosses, lichens do not contribute much to the attenuation of ground heat fluxes despite having low thermal conductivity, due their low thermal capacity[45,142]. Spatiotemporal patterns of organic soil layers such as peat, and thus thermal properties of the soil, are strongly controlled by microtopography, permafrost characteristics and hydrology[4,29,47].

[H2] Balance of winter and summer effects

While in summer shallower thaw depths are found under both low and tall shrub canopies[5] relative to the understory of mosses and lichens (**Table 2**), mean annual soil temperatures tend to be warmer under increasingly tall shrub canopies[5,6,115,145]. This annual warming effect can be related to several observations. First, winter warming tends to be stronger than summer cooling in absolute terms[5,6,115]. For instance, experimental artificial canopies of 70 cm led to 2°C cooling in summer but 5°C warming in winter[6]. Secondly, the winter season is much longer than the summer season at high latitudes. The resulting year-round warming has been proposed to contribute to permafrost degradation in the long run due to gradual increases of permafrost temperatures[5]. However, most assessments of vegetation effects on permafrost focus on topsoil temperatures and little is known about the relative impact of winter warming and summer cooling at soil depths deeper than 20cm. Lastly, effects of vegetation types other than shrubs (such as graminoids, mosses or mixed vegetation) on year-round annual ground temperatures have not been quantified as extensively[45]. Given the importance of canopy height, density and structure to the relative importance of snow processes and canopy heat flux partitioning[3,7,21,100,119,125,133], different vegetation types and plant species are likely to have different balances of winter warming and summer cooling.

An additional knowledge gap is the variability in balance between summer cooling and winter warming of soils varies across diverse permafrost environments. The vegetation-permafrost feedback mechanisms described in this section all depend critically on local-scale landscape structure. For instance, micro- and meso-topography are important factors affecting permafrost dynamics, as even small elevation gradients affect snow depth, surface temperature, soil aeration, soil moisture, soil fertility, the length of the growing season, and depth of thaw[21,43,125,146]. This covariation is an integral part of tundra ecosystems[29,43,47] and could contribute to differences reported in the literature for field-observed impacts on permafrost integrity of various vegetation types[145,147] (Table 2, Fig. 4). Attributing observed changes in soil temperatures or permafrost to particular mechanisms remains challenging, as it requires controlling for a large number of potential influences and interactions[10]. Replication of experimental studies across microtopographical gradients and Arctic regions over multiple growing seasons and continued cross-site synthesis should shed light on the emerging behaviour of permafrost under vegetation changes across different permafrost (micro)environments.

[H1] Vegetation dynamics and abrupt thaw

Permafrost thaw depends not only on the thermal properties of vegetation and soil organic matter but also on the ground ice content of the near-surface permafrost, which determines whether thaw will be gradual or abrupt[16,148]. While active layer deepening improves nutrient availability and drainage, thereby generally improving plant growing conditions and accelerating vegetation succession[18-20] (**Fig. 1**), abrupt thaw can temporarily remove or kill vegetation, delaying or altering the direction of vegetation succession[10,21,22].

Abrupt thaw can only take place when there is excess ice near the permafrost surface. Permafrost ice contents can be as high as 75-90% by volume in the surface layers of the permafrost[16,149]. Ice melting can lead to soil subsidence, altering tundra land-forms and topography at multiple spatial scales, a process also referred to as thermokarst[16,148]. On slopes, thermokarst triggers hillslope processes such as thaw slumps, thermal erosion gullies and active layer detachments[16,76,148,150]. In poorly drained lowland terrain, the resulting changes in surface hydrology can initiate a positive feedback loop, where greater heat diffusivity in wet soils leads to further thawing and melting of ice and vegetation and soil collapse[4,16,21,47,139,151]. Within the Arctic biome, ice-rich permafrost is mostly located in poorly drained lowland landscapes along the Arctic coasts (**Supplementary Figs. 2 & 3, Supplementary Table 4**). Thus, ice-rich permafrost regions can be expected to be most sensitive to permafrost thaw dynamics, which is confirmed by the strong association of the abrupt thaw-driven vegetation change trajectory and ice-rich permafrost occurrence such as in coastal lowlands (**Figs. 3b, c**). As about 20% of Arctic land permafrost is vulnerable to abrupt thaw[152], further climate warming can severely impact the tundra landscape including vegetation.

[H2] Vegetation disturbance and abrupt thaw

Abrupt thaw can be triggered by changes at the tundra surface that abruptly alter the amount and rate of heat transported from atmosphere to soil or remove insulating soil and vegetation layers. Warm summers, particularly when combined with elevated summer precipitation can initiate thaw processes by increasing the amount of available thermal energy[140,141,150] and the rate[139,140,153] at which this energy is transported through the soil (**Fig. 4**). Abrupt thaw can also be forced by extreme winter precipitation[22,44] when a thick, low density snowpack insulates the soil against cold air temperatures[123,154]. The effect of high snowfall on thaw depths can surpass that of air temperatures and can last for multiple years, as is currently evident in Eastern Siberia[155]. Moreover, in the spring following a winter with exceptionally high snowfall, waterlogging can cause large-scale destruction of the vegetation cover[156]. Waterlogging and vegetation mortality can in turn promote further permafrost thaw[16,21]. Finally, wildfires, such as the large fire near Alaska’s Anaktuvuk River, can initiate or accelerate abrupt thaw as the fire removes the protective vegetation and soil organic layer, allowing heat penetration to greater depths[90,157]. These natural processes illustrate the vulnerability of ice-rich permafrost terrain to climate anomalies and vegetation disturbance.

The detrimental effect of vegetation removal or disturbance on permafrost integrity is supported by various manipulation studies (**Table 2**). In general, the removal of a vegetation component (shrub canopy, but also moss and organic layers) increases thaw depths, soil temperature and soil temperature amplitude in summer[2,6,21,111,112]. Addition of moss or litter layers and introduction of artificial canopies tends to have an opposite effect[109,110]. Disturbance of vegetation can trigger positive feedback loops leading to larger scale degradation of permafrost and vegetation, as illustrated by experimental removal of shrub canopies in the Siberian lowland tundra[21]. The latter led to increased thaw depths, which in turn resulted in soil subsidence due to melting of thin ice lenses. Depressions that evolved from ice melting effectively trapped snow and water which contributed to further thawing, water ponding and progressive shrub mortality[21]. As the frequency and scale of abrupt thaw has been increasing over the past decades[68,134,153,158-161], it is unclear to what extent vegetation succession after abrupt thaw can facilitate new ice formation and partly offset the impact of abrupt thaw at a landscape scale.

[H2] Recovery of vegetation and permafrost

Generally, abrupt thaw is followed by recovery related to vegetation succession. Succession mechanisms strongly depend on new hydrological conditions after abrupt thaw. If abrupt thaw leads to ponding (such as thermokarst ponds, pits and troughs), aquatic plant species can establish, often followed by colonization by peat moss (*Sphagnum*)[46,47,162]. Progressive accumulation of organic matter and peat over decades to centuries can elevate the surface above the water table[47], providing a substrate for colonization by terrestrial plants, including shrubs[46]. The formation of an organic layer above the water table also reduces snow accumulation in winter and increases thermal insulation in summer as the top layer dries out[47,111]. The latter enables renewed formation of an ice-rich permafrost layer (syngenetic ground ice formation[163]) and subsequent ground heave, further elevating the surface above the ponding water[46,47,131]. If abrupt thaw does not lead to ponding, for instance, thaw slumps on hillslopes, shrubs expand rapidly on disturbed bare ground[97,99,164], resulting in a strong greening trend[76]. Similar successions can be observed in larger ponds and lakes, which can both slowly fill in with wetland vegetation or drain abruptly after thawing of permafrost increases hydrological connectivity[16,165-167]. Drainage of thermokarst lakes leads to renewed ground ice aggradation[167] and enables vegetation re-establishment, which manifests as pronounced spectral greening[166.] The net effect on a landscape scale and consequences for climate feedback likely depend on the balance between frequency and magnitude of disturbances and recovery rates of vegetation and permafrost.

[H2] Degradation and recovery rates

Timescales for complete vegetation and permafrost recovery are poorly quantified under the current climate, let alone in a rapidly warming Arctic. These timescales also depend on the magnitude of the disturbance[151]. Thermokarst features generally form within weeks to decades[10,16]. In small, shallow thaw ponds with drowned low shrubs, sedges can colonise the new open water within 8 years followed by *Sphagnum* moss establishment. The latter results in a reversal of the increased thaw depths and some initial recovery of permafrost on very short timescales[46]. Complete recovery of permafrost and re-establishment of woody vegetation however might take at least multiple decades[46,47,76,150,151,164] for small-scale abrupt thaw (such as small tundra ponds, shallow ice wedge degradation or smaller thaw slumps) to centuries or millennia after large-scale degradation (such as thaw lakes, advanced ice wedge degradation and large thaw slumps)[150,151,167,168].

Climatic conditions, ground ice content, sediment characteristics and landscape physiography further influence mechanisms and timescales associated with recovery rates of permafrost[4,47,151,167]. The extent, ice content and structure of newly aggraded permafrost are often different from those prior to disturbance[11,47,151,167], and some permafrost degradation is irreversible[4,169]. In relatively warm subarctic permafrost peatlands, permafrost recovery might not occur in the current climate and species composition can shift permanently under the resulting hydrological changes[169]. Stabilisation can also be halted if thermokarst is accompanied by continued large-scale erosion in fluvially incised and coastal environments[159].

Such irreversible processes illustrate the potential limit to the resilience of Arctic ecosystems. If the scale or frequency of disturbance outpaces those of vegetation and permafrost recovery, the consequences can cascade beyond the scale of the initial disturbance. Once disturbance prevails over recovery, it can lead to (quasi-)permanently changes in distribution and connectivity of ecosystems across the Arctic landscape[27,170]. The non-linear response is most evident when changes in topography or soil hydraulic conductivity alter water drainage patterns, as changes in water flow paths can lead to formation of new thaw lakes, disappearance of existing thaw lakes or changes to river discharge regimes[44,171]. Improved understanding of when and where these tipping points could be reached is one of the big ongoing challenges for Arctic research[27,170].

[H1] Summary and future perspectives

Large-scale satellite observations indicate widespread greening in the Arctic tundra region, supporting field-observed vegetation changes and other circumarctic evidence of change ,including increased shrub cover, change in plant communities and an increase in tundra plant height[38,48,172]. Browning events, such as abrupt thaw and tundra wildfires, result in loss of vegetation, but are currently too short-lived and too small-scaled to substantially impact the multi-decadal greening trend. Spectral greening is generally related to gradually improving environmental conditions for plant growth[51], but can also be related to vegetation recovery after browning events[50,76], making spectral trends sensitive to the time-interval over which they are assessed[50]. Field studies confirm that increased cover of woody vegetation remains the prevailing trend in Arctic tundra ecosystems. Ice content of the permafrost appears to be an important local control on tundra vegetation shifts, which can be used to further improve Arctic vegetation models by taking ice content information into account. Tree encroachment predominantly takes place in upland tundra regions low in permafrost ice content, whereas in permafrost regions with higher ice content, vegetation succession following abrupt thaw is the dominant reported change. However, there is still limited information on the timescales of vegetation and permafrost recovery after abrupt thaw.

Many field studies are concentrated in northern Alaska and north-western Canada, while highly vulnerable regions in Arctic Russia, such as the ice-rich coastal Siberian lowlands, remain largely unexplored or otherwise underrepresented in English literature[92,152]. In the Russian Arctic in particular, ice-rich soils often coincide with carbon-rich Yedoma deposits **[G]** [173], making the most unstable regions the most sensitive regarding potential greenhouse gas release. Similarly, the high Arctic remains underrepresented[38,48], and establishment of monitoring programs in the Canadian Archipelago—which has shown strong browning[49] and rapid permafrost degradation[68]—and northern Greenland is highly encouraged[92]. While abrupt thaw can impact local infrastructure[174], the reverse, human activities resulting in vegetation damage, can lead to abrupt thaw[160,175].

Empirical data from field and remote sensing at multiple scales are essential for improving the vegetation and permafrost simulation models that are currently used to predict future greenhouse gas emissions from a warming Arctic. Modelers should take tundra ecosystem changes including abrupt thaw but also gradual active layer increases into account using real-world data to help parameterize or constrain ecosystem models[10,69,176,177]. Empirical data also provide support for ecological conservation and environmental management to reduce the ecological vulnerability of the Arctic tundra ecosystem and sustain the livelihoods of Arctic peoples[1,14].We describe three main challenges for Arctic tundra ecosystem research to help achieve these goals.

Understanding how tundra ecosystems will respond to the expected changes in surface wetness requires improved spatial resolution of remote sensing moisture datasets, such as from microwave remote sensing[105], that can capture relevant landscape heterogeneity. Hydrological aspects are relatively poorly covered in field research, despite large anticipated changes in tundra hydrology. Both the amount of precipitation and the ratio of precipitation that falls as rain rather than snow are anticipated to increase in the Arctic[178] and can be expected to increase permafrost thaw[179]. The effects of precipitation on the thermal regime are further regulated by (micro)topography. Accumulation of precipitation in downslope landscape positions can promote localized permafrost thaw and methane emissions[141,179] and is known to contribute to the browning signal in certain regions of the Arctic[78]. In contrast, in uplands and in lowlands where water flow is impeded by subsurface ice structures, permafrost thaw can promote increased subsurface drainage[16,44,165], resulting in drier soils[44]. Whereas time series of surface soil temperatures have been measured in many locations (**Table 2**) using miniature temperature loggers, soil moisture is not as well-monitored. Improved soil moisture datasets with high spatial and temporal resolution would be a crucial step forwards in our understanding of Arctic ecosystems in a changing climate.

To properly assess the long-term net effect of vegetation on permafrost thaw, there needs to be an improved understanding of interactions of vegetation with soil thermal-hydrological properties, (micro)topography and deeper soil and permafrost temperatures rather than topsoil temperatures alone. Ecologically and climatologically informed manipulation experiments of vegetation cover should explicitly monitor geophysical changes across multiannual timescales, deeper soil and permafrost depths and diverse permafrost environments and microtopography. Since experimental manipulation of a single driver might not always be representative of real-world changes, comparison with long term monitoring studies and experimental studies that manipulate multiple drivers is recommended[48]. The latter will help to disentangle the high degree of interrelatedness between vegetation, water, permafrost and topography that characterizes Arctic environments. While geophysical studies tend to pay little attention to vegetation, ecological studies do not always account for soil thermal and hydrological aspects, and the two should be more integrated.

A final challenge is in upscaling the many - often highly localized - interactions to larger spatial and temporal scales. While increasing spatial and temporal resolution of panarctic satellite- or model-based datasets has led to substantial progress on this front, controlling for a very large number of potential influences and interactions in models is notoriously challenging[10]. Instead, replication of experimental studies across microtopographical gradients and Arctic regions over multiple growing seasons and continued cross-site synthesis could shed light on the emerging behaviour of permafrost under vegetation changes across different permafrost environments.

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Author contributions

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Competing interests

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Key points

- Expansion of shrub vegetation is by far the most reported field-observed vegetation change in the Arctic tundra region, contributing to field- and satellite-observed Arctic greening.
- Spectral greening trends are sensitive to the spatial and temporal scales over which they are observed; ground-truthing via field studies thus remains indispensable for interpretation.
- Tree and shrub establishment occur primarily in warming upland regions on ice-poor permafrost, whereas abrupt thaw followed by vegetation recovery is relatively abundant on lowlands with ice-rich permafrost.
- Geographical coverage of field studies is concentrated in western North America, leaving large areas of Arctic tundra in High-Arctic Canada and Siberia poorly characterized.
- Increasing vegetation cover and height affect soil thermal regimes, with warming in winter and cooling in summer. Integration of ecological and geophysical knowledge is necessary to assess long-term net effects.

- While disturbances of vegetation and permafrost can be compensated by strong internal soil-vegetation feedbacks, tipping points and large-scale ecosystem collapse could occur once disturbances exceed capacity for recovery.

Tables

Table 1 Vegetation structure in bioclimate subzones.

Bioclimate subzone[31]	Mean July temp (°C)[31]	Vertical structure of plant cover[31,35]	Horizontal structure of plant cover[31,35]	Visualisation of plant cover* [31]
A	0-3	Mostly barren. In favourable microsites, one lichen or moss layer <2 cm tall, very scattered vascular plants barely exceeding the moss layer.	<5% cover of vascular plants, up to 40% cover by mosses and lichens.	[Insert t1.1]
B	3-5	Two layers: a moss layer 1-3 cm thick and a herbaceous layer, 5-10 cm tall, with prostrate dwarf shrubs <5 cm tall.	5-25% cover of vascular plants, up to 60% cover of cryptogams.	[Insert t1.2]
C	5-7	Two layers: a moss layer 3-5 cm thick and a herbaceous layer 5-10 cm tall, with prostrate and hemi-prostrate dwarf shrubs <15 cm tall.	5-50% cover of vascular plants, open patchy vegetation.	[Insert t1.3]
D	7-9	Two layers: a moss layer of 5-10 cm thick, and a herbaceous or dwarf shrub layer 20-50 cm tall, sometimes with a low-shrub layer to 80 cm.	50-80% cover of vascular plants, interrupted closed vegetation.	[Insert t1.4]
E	9-12	Two to three layers: a moss layer 5-10 cm thick, a herbaceous or dwarf-shrub layer 20-50 cm tall, and sometimes a low-shrub layer to 80 cm	80-100% cover of vascular plants, closed canopy.	[Insert t1.5]

*Grey: barren; yellow: graminoid; light green: dwarf shrub; dark green: shrub; blue: wetland.

Table 2: *Field observations of relationships between Arctic tundra vegetation and soil thermal and permafrost conditions (*

Study area and reference	Bioclimate subzone*	Winter Effect **	Winter Mechanism	Summer Effect **	Summer Mechanism
Meta-analyses					
Synthesis of soil temperature data from 87 tundra sites[5]		Pos		Neg	
Observational Studies					
Faddeyevsky Island, Russia (75N, 144E)[180]	B	-		Neg	Insulating moss layer
Prudhoe Bay, USA (70.23N, -148.42E) [47]	C	Neg	Sparser vegetation associated with thermokarst depressions, which accumulate snow	Neg	Insulating organic layer
Howe Island, USA (70.30 N, 147.98 W) [145]	C	Pos	Canopy snow trapping	Neg	Insulating organic layer
Franklin Bluffs, USA (69.67 N, 148.72 W) [145]	D	Pos	Canopy snow trapping	Neg	Insulating organic layer
Happy Valley, USA (69.13 N, 148.83 W) [145]	E	Pos	Canopy snow trapping	Neg	Insulating organic layer
Indigirka lowlands, Russia (70.83N, 147.49E) [46]	E	-		Neg	-
Illisarvik basin, Canada (69.48N, -134.59E) [116]	E	Pos	Canopy snow trapping	Neg	-
Ayiyak River, USA (68.83N, -152.52E) [7]	E	Pos	Canopy snow trapping	Neg	Soil shading, insulating organic/moss layer
Kuparuk and Sagavanirktok Rivers, USA (68.76N, -148.87E) [117]	E	Pos	Canopy snow trapping, talik formation	-	-
Trail Valley Creek research station, Canada (68.74N, -133.50E) [45]	E	Pos	Canopy snow trapping	Neg	Complex effect of snowmelt timing
Siksik Creek watershed, Canada (68.50N, -133.75E) [114]	E	Pos	Canopy snow trapping	Pos/ Neg	Snowmelt timing, vegetation and microtopography
Kharp, Russia (66.83N, 65.98E) [97]	E	Pos	-	Neg	-
Council, USA (64.88N, -163.65E) [8]	E	0	Interactions between canopy snow trapping and branch protrusion	Neg	-
Kashunuk , USA (61.38N, –165.47E) [26]	E	Pos	-	Neg	-
Tutakok, USA (61.25N, -165.49E) [26]	E	Pos	-	Neg	-
Manokinak, USA (61.20N, -165.07E)[121]	E	Pos	-	Neg	-
Izaviknek Hills, USA (61.30N, -162.75E) [181]	E	-	-	Neg	-
Tutakoke River, USA (61.20N, -165.40) [182]	E	-	-	Neg	Sparser vegetation is associated with thermokarst depressions
Mackenzie River Delta, Canada (68.26N - 69.06N)[100]	E/ s	Pos	Canopy snow trapping	Neg	Delayed snowmelt, soil shading

Abisko, Sweden (68.350N, 18.816E) [111]	s	-	-	Neg	Reduced thermal conductivity and moisture under moss
Tasiapik Valley, Canada (56.57N, -76.49E) [113]	s	-	Shrub protrusion, winter snow melting events	-	-
Hudson Bay coast, Canada (56.33N, -76.33E) [118]	s	Pos	Canopy snow trapping	Neg	Soil shading, insulating moss layer
Manipulation Studies					
Indigirka lowlands, Russia (70.83N, 147.49E) [2]	E	0	No effect on snow depth	Neg	Soil shading
Adventdalen, Svalbard (78.17N, 16.12E) [110]	A	0	-	Neg	Insulating moss layer
Indigirka lowlands, Russia (70.82N, 147.48E) [21]	E	-	Shrub removal resulted in thermokarst depressions, which accumulate snow	Neg	Shrub removal resulted in thermokarst
Indigirka lowlands, Russia (70.82N, 147.47E) [112]	E	-	-	Neg	Insulating moss layer
Abisko, Sweden 68.350N, 18.816E) [111]	s	0	-	0	Insulating moss layer
Ruby Range Mountains, Canada (61.22N, -138.28E) [6]	s	Pos	Canopy snow trapping	Neg	Soil shading
Kluane Lake, Canada (61.22N, -138.28E) [109]	s	Pos	-	Neg	Canopy shading and interception.

** A-E refer to CAVM bioclimate zones, see **Table 1.** s = "Tundra site in subarctic climate zone".*
*** Identified effect of vegetation on soil temperatures and/or permafrost conditions in summer or winter. Pos = warming, Neg = cooling, 0 = no effect, - = Not examined.* Full descriptions can be found ine in **Supplementary Table 5**.

Figure Legends

Figure 1. Vegetation change trajectories. **a|** Changes in vegetation in well-drained, ice-poor Arctic tundra. **b|** changes in vegetation in poorly-drained ice-rich Arctic tundra. On relatively well-drained sloping terrain on ice-poor permafrost, tussock tundra, consisting of tussock-forming sedges and some dwarf shrubs, is the dominant vegetation type. Under conditions of gradual permafrost thaw, vegetation can become more productive and shrubs can establish on the relatively dry soils. In case of poorly drained terrain underlain by permafrost with ice wedges or ice lenses, permafrost degradation leads to mortality of dwarf shrub vegetation owing to drowning, followed by establishment of aquatic sedges in the new or deeper open water.

Figure 2. Spatial patterns in field-observed vegetation changes and associated NDVI dynamics. a| Dominant field-observed vegetation change trajectory (green, blue and grey shapes) and NDVI trends (colour), as evident from Theil-Sen regression slopes of annual maxima in MODIS 250m resolution greenness over the period 2000-2020. Statistically Insignificant trends are depicted as zero, with smaller symbols. Blue shades indicate non-monotonic increases whereas green shades indicate monotonic increases, as determined by a Mann-Kendall test (see Supplementary methods).The green area represents Arctic vegetation zones A-E above the tree line, as defined in the Circumpolar Arctic Vegetation Map[31]. **b|** Observed frequency of main field-observed vegetation trajectories. **c|** MODIS NDVI trend per vegetation trajectory. Values indicate the number of field sites per vegetation change category. Shrub expansion is the dominant field-observed vegetation change, but does not contribute more to NDVI trends than other vegetation changes (ANOVA, $F(4,55) = 0.287$, $p = 0.885$).

Figure 3. Distribution of field-observed vegetation change trajectories over the Arctic. a| Spatial distribution of field sites over CAVM bioclimate zones[31] (left panel), and contingency tables of vegetation change trajectory with bioclimate zones (right panels). The size of dots in the right panel represents the deviation from the expected distribution, quantified as Pearson residuals. The colour represents either fewer (red) or more (blue) observations than expected based on marginal totals. P-values indicate whether two categorical variables are significantly associated based on a Fisher's exact test. Bioclimate zones A and B were excluded due to underrepresentation (n=1). See Supplementary Figures 2-4 and Supplementary Table 4. **b|** as in **a**, but over CAVM landscape types[31]. Hills and mountains were aggregated to "upland" terrain. **c|** as in **a**, but for permafrost extent types and ice content[106]. Discontinuous permafrost with medium and low ice content was aggregated to "discontinuous permafrost", continuous permafrost was further subdivided based on ice content.

Shrub expansion is concentrated in upland terrain, whereas thermokarst-driven succession is concentrated in ice-rich lowland terrain.

Figure 4. Effects of shrub canopies on permafrost thaw depth. Black arrows indicate effects related to vegetation, snow and soil (+ for positive, - for negative). Dashed arrows indicate net effects across causal dependencies, where blue indicates positive net effects on permafrost integrity and red negative net effects. Ground heat flux refers to a heat flux from atmosphere to soil, where the reverse situation (soil to atmosphere) is interpreted as a negative flux. Shrub canopies influence permafrost conditions through effects on snow, heat fluxes and soil.

Glossary

Tall shrubs: erect shrubs, generally 2m or talleroften growing on more fertile sites such as flood plains. Species comprise mostly deciduous species such as *Salix* and *Alnus* species

Dwarf shrubs: low-statured shrubs, generally less than 1m tall, mostly evergreen ericaceous shrubs, but also deciduous shrub species such as *Betula nana.*

Graminoids: plant species with an erect grass-like growth form, encompassing both true grasses and sedges.

Active layer: the top layer of soil which overlies permafrost, thawing in summer and refreezing in winter.

Normalized Difference Vegetation Index (NDVI): a spectral vegetation index that is sensitive to the green biomass, generally correlating with plant properties such as leaf area index.

Spectral greening: Increasing (positive) trends in NDVI, or other satellite-derived vegetation indices.

Spectral browning: Decreasing (negative) trends in NDVI.

Paludifying: gradual conversion of forest or shrubland to peatlands.

Yedoma deposits: wind-blown deposits from the last ice age, often rich in ground ice and soil organic matter.

TOC summary

Greening and vegetation community shifts have been observed across Arctic environments. This Review examines these changes and their impact on underlying permafrost.